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Research article

Herbicide effectiveness in controlling invasive plants under elevated CO_2: Sufficient evidence to rethink weeds management

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ABSTRACT

Previous studies have reported that chemical weed control will be less effective for some weed species under future atmospheric CO_2 concentrations. Such reductions in plant sensitivity to herbicides under elevated CO_2 may be due to greater biomass accumulation and differences among growth types. However, these studies have been limited to few growth types (herbaceous and grass species) and to a single herbicide (glyphosate).

This study tested a more extensive range of weed species (both in number and growth form) and herbicides to assess general patterns of plant response. We grew 14 environmental weed species representing four different growth forms (grasses, herbs, shrubs and vines), that are commonly found in south-eastern Australia, under ambient (380 ppm) and elevated (550 ppm) CO_2 concentrations. We then applied the recommended and double-recommended concentrations of two herbicides: glyphosate and fluroxypyr-meptyl. We found that responses of the weed species to herbicide under elevated CO_2 were species-specific. However, the C_3 grasses tended to be the most sensitive to herbicide application followed by the herbs and C_4 grasses while shrubs and vines demonstrated the highest resistance. Our results highlight the need for broader testing to determine the species most likely to exhibit increased tolerance to herbicide in the future in order to improve management options beforehand and thus offset a future liability.

1. Introduction

It has been predicted that ongoing climate change may advantage many weedy plant species due to their broad environmental tolerances and capacity for rapid dispersal and colonisation (Bajwa et al., 2018; Carboni et al., 2015; Mgidi et al., 2007; Seebens et al., 2015); although this may not be true for all weed species (O'Donnell et al., 2012; Roger et al., 2015). Furthermore, rising atmospheric CO_2 concentration and associated changes in disturbance regimes (*e.g.*, increased frequency and intensity of flood, drought and fire events), are likely to increase the invasion success of many weed species (Diez et al., 2012; Fernandino et al., 2018; Manea et al., 2016; Sorte et al., 2013; Sutherst, 2000). Therefore, weed management under future climates will need to incorporate measures to identify species likely to become problematic due to climate change, in addition to assessing and accounting for the associated risks (Downey et al., 2010a). Weed management must also put in place measures to mitigate against any potential adverse effects that may impact on the way by which weed species are currently managed *i.e.,* through physical, biological and chemical means, to ensure weed management adapts to the challenges associated with future climate change (Leishman and Gallagher, 2015). Given that chemical control using herbicides is the most widely used weed management technique worldwide (Fernando et al., 2016), there has been surprisingly little attention given to how the chemical control of weeds may be altered under future climate conditions (Dukes, 2000; Hellmann et al., 2008; Sutherland et al., 2017; Sutherst, 2000).

Rising atmospheric CO_2 concentration is one of the best documented global changes of the past half century (Jiménez et al., 2018; Prentice et al., 2001). As a result, plant responses to elevated CO_2 have been extensively studied over the past four decades (Ainsworth and Long, 2005; Amthor, 1995; Leakey et al., 2009; Morison and Gifford, 1984). These responses include a reduction in stomatal conductance and transpiration, improved water and nitrogen use efficiency and higher rates of C_3 photosynthesis (Leakey et al., 2009). Despite this, there have been very few studies that have attempted to link these biochemical, physiological, metabolic, and morphological shifts under elevated CO_2 to changes in herbicide efficacy on weed species (Fernando et al., 2016; Varanasi et al., 2016). Early studies that

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addressed this question (Archambault et al., 2001; Manea et al., 2011; Ziska et al., 2004; Ziska and Teasdale, 2000) reported that weedy grass and herbaceous species tended to display increased tolerance to the herbicide glyphosate when grown under elevated CO_2 (Table S1). However, subsequent studies (e.g., Jabran, 2016; Marble et al., 2015; Zhang et al., 2015) examining a different set of weedy grass, herbaceous and sedge species provided limited evidence to support these initial studies (Table S1). In addition to this, the mechanism by which herbicide efficacy may be altered under elevated CO_2 remains unclear. Perhaps the simplest explanation is that an increase in biomass under elevated CO_2, particularly in belowground biomass, may have a dilution effect on herbicides (Ziska et al., 1999; Ziska and Teasdale, 2000). However, Fernando et al. (2016) have subsequently argued that such morphological changes alone cannot explain the underlying mechanisms of herbicide resistance and that biochemical and physiological changes must also be examined. For example, altered enzymatic activity, pigment production, increased starch levels in C_3 plants and decreased protein levels have been shown to interfere with a range of herbicides (Patterson, 1995). This lack of consensus highlights the need for further research to determine the underlying mechanism determining herbicide tolerance under elevated CO_2. This may then enable us to shed some light on the species-specific responses we have observed to date. In a broader context, it is essential to address this knowledge gap as weed management under climate change not only has to account for changes in plant growth and performance but also potential changes in herbicide effectiveness, given that any increase in herbicide tolerance would have significant implications for future weed management options (Ziska and Dukes, 2011).

Of the thousands of weed species globally, we are aware of only 21 weed species that have been examined for changes in herbicide tolerance under elevated CO_2 (Table S1). Furthermore, these 21 weeds are confined to either grasses or herbaceous species which are weedy mostly in agricultural systems; a focus which has flowed through to a restricted discussion on the outcomes, focusing on crop-weed management (Naidu, 2015; Varanasi et al., 2016; Ziska, 2016; Ziska and McConnell, 2015). It is not feasible to investigate every weed species and herbicide-specific responses to elevated CO_2 and consequently broader approaches to understanding the likely outcomes are required. Thus, the aims of this study were two-fold. Firstly, to extend the existing knowledge on herbicide efficacy under elevated CO_2 to a larger number of weed species by assessing growth and survival of 14 common environmental weed species of south-eastern Australia treated with recommended herbicides under ambient and elevated CO_2 conditions. These 14 weed species span a wide range of growth forms (C_3 and C_4 grasses, herbs, vines and shrubs) to provide a more representative assessment of weed flora. Secondly, to investigate if a higher dose of herbicide would be needed in the future to offset the effects of elevated CO_2 on herbicide tolerance. We hypothesized that herbicide efficacy under elevated CO_2 is likely to decrease.

2. Materials and methods

2.1. Species selection

The 14 selected weed species encompassed a range of plant families and growth forms (Table 1). *A. cordifolia*, *A.s aethiopicus* and *L. camara* are listed as Weeds of National Significance in Australia while *A. adenophora* is a declared weed in some areas of Australia. All of the other species are considered environmental weeds (Downey et al., 2010b; Skarratt et al., 1994). Two of these 14 plant species (*C. gayana* and C. *clandestinum*) are C_4 species and the remainder are C_3 species. The 14 environmental weed species were represented by two vine, three herb, four shrub and five grass species (Table 1).

2.2. Plant preparation

Plants were propagated from seed, or cuttings or tubers when seeds were not available, which were all collected in the greater Sydney region, Australia (Table 1). Seeds, sampled from multiple plants, were germinated on moist filter paper at room temperature. Seedlings at the stage of cotyledon emergence were transplanted into 700 mL pots filled with commercial potting mix (Australian Native Landscapes, Terrey Hills, NSW, Australia) and 10 g of slow release fertilizer (16:3.9:10 N:P:K; Osmocote, Gordon, NSW, Australia). The pots were lined with newspaper to prevent soil loss through the drainage holes. Species propagated vegetatively were planted directly into pots (Table 1). *A. cordifolia* was grown from tubers while *L. camara*, *T. fluminensis,* and *I. indica* were propagated from stem fragments approximately 100 mm long. All plants were grown between December 2011 and July 2012.

2.3. Experimental design

The experiment followed a randomised fully factorial design, with the factors being CO_2 concentration (ambient or elevated) and herbicide treatment (recommended and double recommended label rate). Four glasshouses were used: two at the ambient and two at the elevated CO_2 concentration.

Ten replicates of each weed species for each CO_2 × herbicide treatment combination were grown. These were evenly split between the treatment glasshouses. Additionally, six replicates of each weed species were grown under each CO_2 treatment to assess the biomass allocation of each species at the time of herbicide application. This could not be done after herbicide treatment due to plant mortality. These plants were harvested into their above- and belowground components on the day of herbicide application and oven-dried at 60 °C until the weight remained constant (48–72 h) before being weighed.

Pots were randomly rearranged within the glasshouses each fortnight to minimise any within-glasshouse effects. All pots were evenly spaced to minimise shading from neighbouring plants. As *L. camara* and *I. indica* were propagated from cuttings, they were re-potted into 2.8 L pots after eight weeks and six weeks respectively to allow them ample space for root development. The vine species *A. cordifolia* and *I. indica* were trained onto stakes. Pots were mist watered for one minute four times daily.

The elevated CO_2 treatment was maintained by a dosing and monitoring system (Canary Company Pty Ltd, Lane Cove, NSW, Australia) at 550 ppm, from 6 am to 6 pm, with air continuously circulated within each glasshouse. The elevated CO_2 treatment represents the predicted atmospheric CO_2 concentration by 2030 under most emissions scenarios (IPCC, 2001). The ambient CO_2 treatment was 380 ppm. The glasshouse temperature was set to 17 °C at night and 24 °C during the day.

2.4. Herbicide application

We reviewed the weed control literature and herbicide manufacturer guidelines for recommended application rates of glyphosate and other commonly used herbicides for each of the 14 weed species to determine the recommended or label rate and double rate. Half of the replicates for each of the 14 weed species were sprayed individually with glyphosate (Accensi Pty, Narangba, QLD, Australia) at the recommended concentration or label rate for that species (Table 1) and the other half of the replicates were treated with double the recommended rate (n = 10). In each case, 3 mL of the surfactant LI-700 (Nufarm, Hunter Valley, NSW, Australia) was added per litre of herbicide mixture. Three species (*i.e., T. fluminensis, L. camara* and *A. cordifolia*) were also treated with fluroxypyr-meptyl (Starane Advanced, Dow Agro Sciences, Frenchs Forest, NSW, Australia), at the recommended and double recommended rate (n = 10), as these species

Table 1
Information on nomenclature, family, growth form, propagation method, herbicide application rate and type for the 14 weed study species examined. Recommended herbicide rates used and actual amount of active ingredient applied per plant were in accordance with: a) Glyphosate label; b) Department of Environment and Conservation (2005); c) Prior and Armstrong (2001), and; d) Starane Advanced product label (Dow Agro Sciences). Recommended rates of herbicide 360 glyphosate (G) and recommended rates of 333 fluroxypyr-meptyl (F) used, actual amount of active ingredient applied per plant and number of replicates (n) are reported. Only three species were treated with 333 fluroxypyr-meptyl.

Weed Species	Family	Growth Form	Propagation	Recommended rate of herbicide (mLL^{-1})	Active herbicide ingredient per plant in the recommended rate treatment (mg) and replicates (n)
Ageratina adenophora	Asteraceae	herb	seed	G: 10[b]	G: 36 (n = 10)
Anredera cordifolia	Basellaceae	vine	aerial tuber	G: 20[c]	G: 72 (n = 10)
				F: 3[d]	F: 10 (n = 10)
Asparagus aethiopicus	Asparagaceae	shrub	seed	G: 13[b]	G: 46.8 (n = 10)
Avena barbata	Poaceae	annual grass	seed	G: 10[b]	G: 36 (n = 10)
Bromus catharticus	Poaceae	annual grass	seed	G: 10[b]	G: 36 (n = 10)
Chloris gayana	Poaceae	perennial grass	seed	G: 10[a]	G: 36 (n = 10)
Cotoneaster glaucophyllus	Asteraceae	shrub	seed	G: 10[a]	G: 36 (n = 10)
Ehrharta erecta	Poaceae	perennial grass	seed	G: 10[b]	G: 36 (n = 10)
Ipomoea indica	Convolvulaceae	vine	cutting	G: 10[b]	G: 36 (n = 9–10)
Lantana camara	Verbenaceae	shrub	cutting	G: 10[a]	G: 36 (n = 10)
				F: 3[d]	F: 10 (n = 10)
Cenchrus clandestinum	Poaceae	perennial grass	seed	G: 10[a]	G: 36 (n = 10)
Senna pendula	Fabaceae	shrub	seed	G: 10[a]	G: 36 (n = 10)
Tradescantia fluminensis	Commelinaceae	herb	cutting	G: 13[b]	G: 46.8 (n = 10)
				F: 9[d]	F: 30 (n = 10)
Verbena bonariensis	Verbenaceae	herb	seed	G: 10[a]	G: 36 (n = 9–10)

are commonly treated with this herbicide under recommended best practice bushland management (pers. comm., Ensbey and Johnson, 2009).

Herbicide treatments were applied while the plants were still actively growing (March–June 2012), after 45–121 days of growth (Table S1). On the day of herbicide application, individual plants were taken outside the glasshouses and placed in a well-lit, ventilated area. Herbicide was only applied on days that were predicted to be precipitation-free and with no or light winds. Plants within the same herbicide treatment were spaced at least 0.8 m apart from each other to avoid spray drift between treatments; plants were spaced at least 4 m apart. Once the foliage of each plant was completely dry (*i.e.,* from any residual moisture from the glasshouse), the plants were sprayed using a hand sprayer between 8:00 and 11:00 am. Each plant received 10 mL of either the recommended rate or double the recommended rate which was sufficient to cover the foliage of the entire plant to the point of the herbicide running off. The amount of active ingredients that each plant received is listed in Table 1. The herbicide treatment plants were left outside to dry completely before being returned to their respective glasshouses. Watering was withheld for 6 h after herbicide application to ensure the maximum efficacy for all herbicide applications (types and rates). All control treatment (or non-herbicide) plants were left in the glasshouses and mist watered.

Herbicide and control treatment plants were monitored weekly after herbicide application for survival. A plant was considered alive if it still had live tuber (*A. cordifolia* only) or leaf material (all other species). After six weeks all plants were visually checked for the presence of living (turgid) roots to ensure that our visual assessment of survival matched the actual survival. All unsprayed control plants survived.

2.5. Data analysis

The survival of weeds was censored weekly for six weeks according to the non-informative censoring assumption of the survival test. Interactive effects of CO_2 and herbicide treatments were evaluated with Cox proportional hazard ratio model for each species (Table S2) using "survival" R package (Cox, 1972; Therneau, 2015). The proportional hazards assumption for Cox regression model fit was tested with diagnostics based on Schoenfeld residuals to test for independence between residuals and time (Grambsch and Therneau, 1994). No violation was detected, with the exception of *T. fluminensis* under herbicide fluroxypyr-meptyl and this was resolved by incorporating census time as an interactive term. The proportional hazard ratios for each species under CO_2 × herbicide treatment were visualized using "survminer" R package (Kassambara et al., 2018).

Statistical differences between ambient and elevated CO_2 treatments of total dry weight and root mass fraction for each species were tested with ordinary least square regression in R software (RStudio Team, 2016; Team, 2017). The assumption of homogeneity in model residuals was centered on zero and assessed visually with no issues detected. Differences in biomass accumulation rates – defined as total biomass divided by days of growth, were assessed visually (Fig. S1). Data are available at Mendeley Data Repository (Waryszak et al., 2018).

3. Results

3.1. Biomass

Biomass, measured as plant dry weight prior to herbicide application, was greater in 11 of the 14 weed species under elevated compared to ambient CO_2 (Table S2). However, this increase was only significant for the perennial C_4 grass *C. clandestinum* (28% increase, $t = 3.57$, $P < 0.05$; Fig. 1, Table S3). In contrast, *C. gayana* (C_4 perennial grass), *L. camara* (shrub) and *V. bonariensis* (herb) produced more biomass under ambient CO_2; this was not significant however. Ten of the 14 weed species allocated more biomass to roots under elevated CO_2; however this was only insignificant for *C. clandestinum* (31% increase, $t = 2.73$, $P < 0.05$, Table S3). Similarly, no difference in the mean biomass accumulation rate (g/day) was observed between plants grown under ambient and elevated CO_2 conditions except for *C. clandestinum* (Fig. S2).

3.2. Survival after herbicide application

At the recommended rate, only *A. barbata* (C_3 grass; glyphosate, $z = -1.95$, $P = 0.05$) and *A. cordifolia* (vine; glyphosate, $z = -2.34$, $P < 0.05$, Figs. 2 and 3) had increased herbicide tolerance under elevated CO_2. In contrast, *S. pendula* (shrub; $z = 2.1$, $P < 0.05$) had decreased tolerance to glyphosate (at the recommended rate) under elevated CO_2 (Table S4, Fig. S1).

As expected, doubling the herbicide rate increased mortality in 9 of the 14 weed species under ambient CO_2 level with grasses such as *C.*

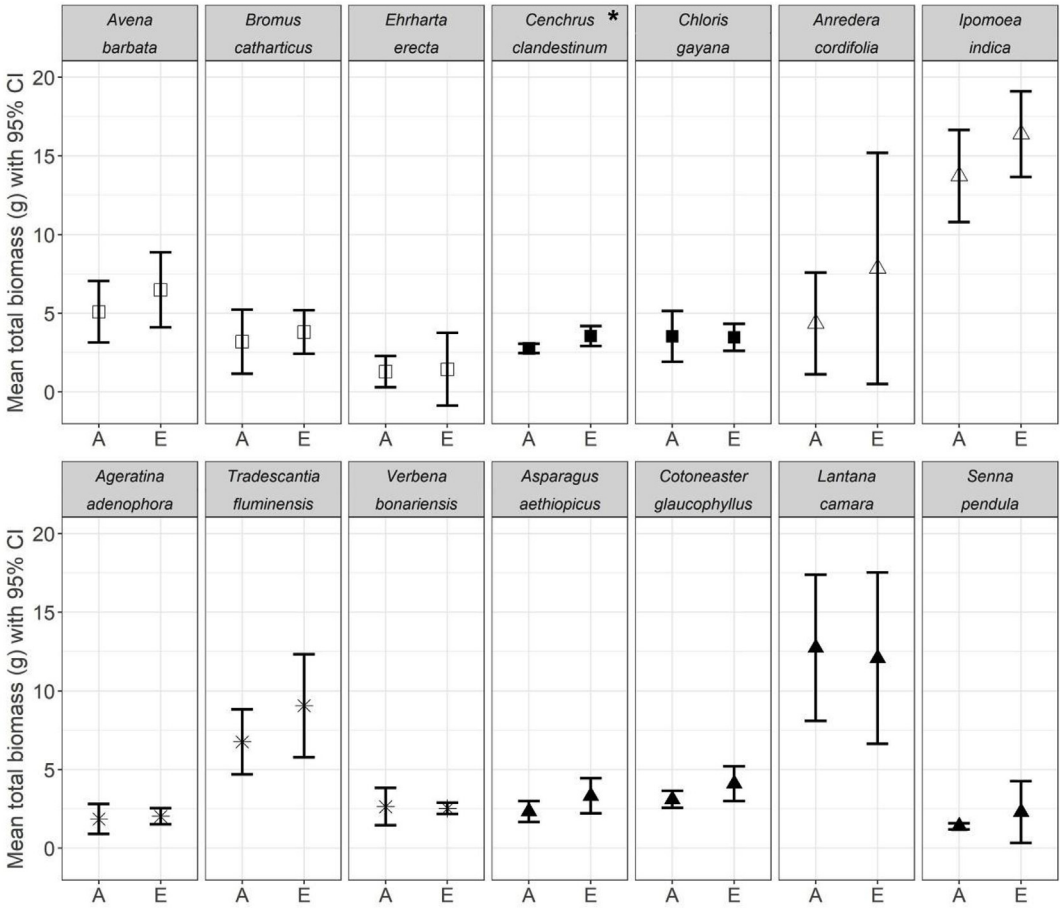

Fig. 1. Effect of CO_2 levels (A – ambient 380 ppm and E – elevated 550 ppm) on total biomass (g) of the 14 weed species (n = 6 replicates): C_3 grasses (open square), C_4 grasses (filled square), herbs (stars), shrubs (filled triangular), and vines (open triangular) ± 95% CI (Confidence Intervals). Asterisk (*) indicates species with significant difference in total biomass between ambient and elevated CO_2 levels.

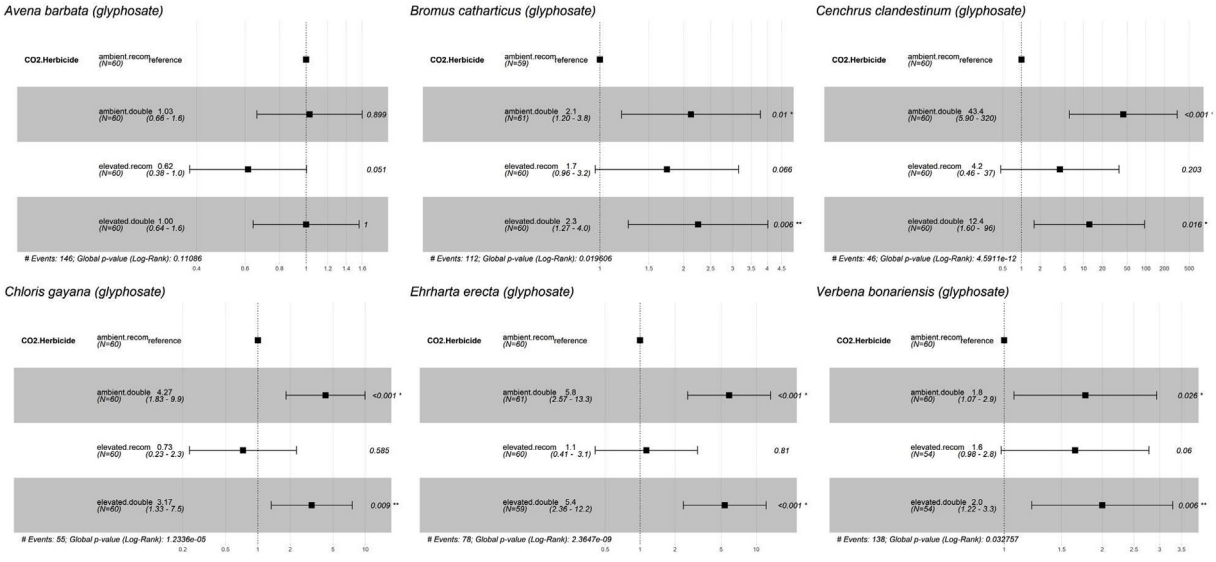

Fig. 2. Proportional hazard ratios (± 95% CI) for weedy grass (*A. barbata*, *B. catharticus*, *C. clandestinum*, *C. gayana*, *E. erecta*) and herb (*V. bonariensis*) species grown under two CO_2 levels: ambient (380 ppm) and elevated (550 ppm) and treated with recommended (recom) and double the recommended (double) herbicide rate. Species survival was censored weekly for six weeks following herbicide application. Hazard ratios values < 1 indicate a higher chance of survival (continue to Fig. 3). .

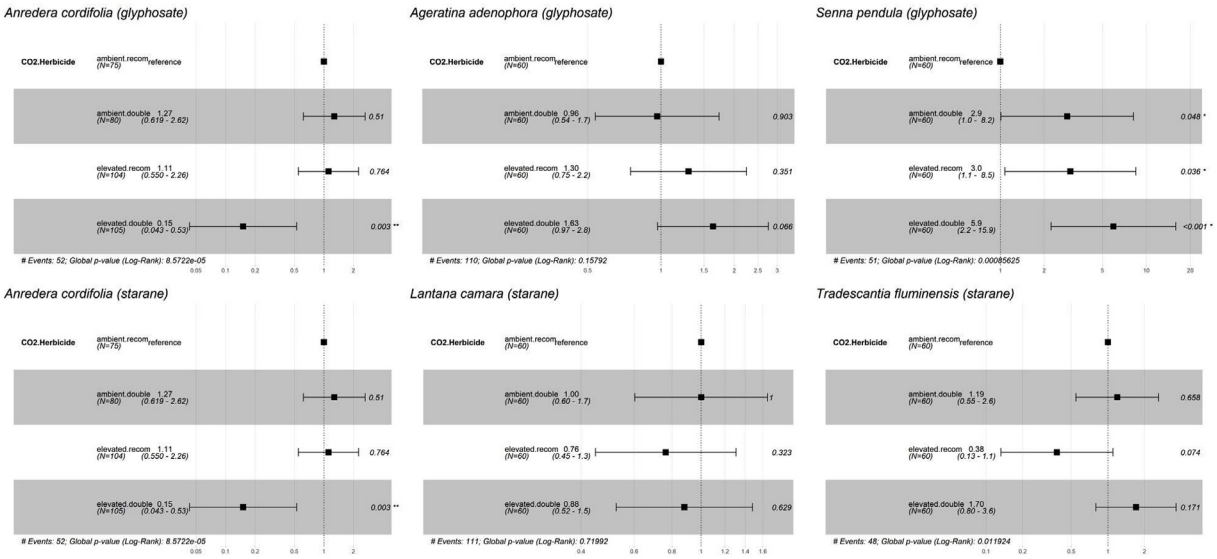

Fig. 3. Proportional hazard ratios (± 95% CI) for weedy vine (*A. cordifolia*), shrub (*L. camara, S. pendula*) and herb (*A. adenophora, T. fluminensis*) species grown under CO_2 × herbicide treatment. Two species showed 100% survival in all treatments (*I. indica* and *T. fluminensis* - glyphosate). Two further species (*A. aethiopicus* and *G. glaucophyllus*) showed 90% and one (*L. camara*) showed 85% survival. These five species are not shown.

gayana (z = 3.36, P < 0.05), *C clandestinum* (z = 3.66, P < 0.05) and *E. erecta* (z = 4.24, P < 0.05) showing the highest sensitivity to double rate of herbicide when compared to the recommended rate (Table S4, Fig. 2). Interestingly, double rate of the herbicide fluroxypyr-meptyl under elevated CO_2 was significantly less effective compared to the recommended rate for *A. cordifolia* (z = −3.70, P < 0.05, Table S4, Fig. 3). Two species showed 100% survival in all treatments using glyphosate (*I. indica* and *T. fluminensis*). In two further species (*A. aethiopicus* and *G. glaucophyllus*) survival was 95% (5% mortality under double glyphosate under elevated CO_2).

4. Discussion

Prior to our study, herbicide efficacy under elevated CO_2 had been determined for 21 weed species (Table S1). These 21 weed species were reported as agricultural weeds that could also become successful invaders in natural environments, for instance: *Chloris gayana* and *Paspalum dilatatum* (Manea et al., 2011). The general aim of this study was to broaden our knowledge base by testing 14 additional weed species from a range of different growth forms and types, all of which are classified as environmental weeds. Similarly to previous studies, our results suggest that herbicide tolerance in weed species grown under elevated CO_2 is species-specific. For example, of the 14 weed species examined, only two species (*A. cordifolia* and *A. barbata*) had significantly greater herbicide tolerance at the recommended herbicide rate under elevated CO_2. The positive effect of elevated CO_2 on herbicide tolerance for the double rate treatment was observed only in one species, *i.e.*, *A. cordifolia* under both herbicides glyphosate and fluroxypyr-meptyl. Although it is clear that a universal trend towards greater herbicide tolerance under future CO_2 conditions is not likely, there is enough evidence to suggest some species may benefit from increased tolerance under future atmospheric conditions. Greater tolerance to herbicides implies additional management challenges, such as use of additional quantities of herbicides, which could have flow-on effects including an increase in herbicide resistence and increased risk of negative impacts on ecosystems (Fu et al., 2018; Taylor and Kumar, 2013). Furthermore, weed populations that have developed resistance to one herbicide are likely to show resistance to other herbicide types (Hicks et al., 2018). Alternative management strategies that involve non-herbicide means (*e.g.*, reducing nutrient inputs, manual control or biological control) may require greater resourcing in the future. From a weed risk management perspective, the consequence of increased herbicide tolerance in weed species in the future should be incorporated into present risk management practices (Downey et al., 2010a). Current weed management practices must consider future risk, especially with the already high occurrence of herbicide tolerance observed to date (Heap, 2017). Hence, it is important that risk estimation models incorporate not only increasing weed resistance to herbicides but also factor in an interactive effect of CO_2 level and herbicide rate before guiding weed control worldwide (Fernando et al., 2016).

4.1. Effect of biomass accumulation on herbicide efficacy

Despite many studies reporting a fertilisation effect on plant growth under elevated CO_2 (Bunce, 2018; Cure and Acock, 1986; Curtis and Wang, 1998; Eamus and Jarvis, 1989; Paudel et al., 2018), our results did not show this pattern. To date, the majority of research on CO_2 concentration effect on herbicide efficacy has tested potential morphological mechanisms, namely that greater biomass production under elevated CO_2 contributes to reduced herbicide efficacy (Manea et al., 2011; Ziska et al., 2004). Increased biomass accumulation rate reported for plants grown under elevated CO_2 may alone suffice to rethink weed control under future atmospheric conditions (Belote et al., 2004; Poorter and Navas, 2003; Ziska et al., 2007). Previous studies have suggested that an increase in biomass may result in a dilution effect thus reducing effectiveness of the herbicide on weeds (Manea et al., 2011). With the exception of *C. clandestinum*, we found no evidence to suggest that enhanced biomass production under elevated CO_2 is related to greater herbicide tolerance.

In the field study by Wu et al. (2018), the biomass response to elevated CO_2 was strongly correlated with amount of nitrogen fertilizer in the soil. The soil used in this study contained slow-release fertilizer that could have limited the plants' growth responses to elevated CO_2. In the field, especially in disturbed soils where nutrient availability is high, for instance after fire (Dean et al., 2015) or clear-cutting (Wang et al., 2018), weed biomass production might be more responsive to elevated CO_2. In a meta-analysis of several hundred observations of plant CO_2 response, Poorter and Navas (2003) found that angiosperms had stronger growth responses to elevated CO_2 than gymnosperms, C_3 species responded more strongly than C_4 species and that within herbaceous C_3 species, fast-growing species responded more strongly than slow-growing species. While our results vary from those of Poorter and

Navas (2003), in that C_3 grasses showed no significant increase in biomass nor in biomass accumulation rate under elevated CO_2, these results suggest the types of weed species that future studies relevant to weed management could focus on.

4.2. Effect of CO_2 concentration on herbicide efficacy

Tolerance of weed species to herbicides under ambient and elevated CO_2 is highly variable, species- and context-specific despite the lack of biomass response to elevated CO_2. For example, of the 14 plant species examined here, one species *i.e.*, *A. cordifolia,* exhibited significantly greater tolerance to both glyphosate rates and double recommended fluroxypyr-meptyl rates at elevated CO_2 in line with previous studies (Archambault et al., 2001; Manea et al., 2011; Ziska et al., 2004, 1999; Ziska and Teasdale, 2000). This is a very worrying outcome as *A. cordifolia* (Maderia vine) is listed as a Weed of National Significance in Australia. Another weed species, *A. barbata* recorded greater tolerance to recommended glyphosate rate under elevated CO_2. Neither of these species had changes in biomass, which suggests that biochemical or other changes, rather than increased biomass accumulation, results in increased herbicide tolerance. For example, plants might reduce stomatal conductance and decrease their stomata number under elevated CO_2 which in turn may compromise the uptake of glyphosate by foliar tissue (Ainsworth and Long, 2005; Nowak et al., 2004; Pathare et al., 2017; Ziska and Teasdale, 2000). Moreover, increased leaf wax deposition and overall leaf thickness under increased CO_2 concentration may further reduce herbicide efficacy (Gamage et al., 2018; Hikosaka and Shigeno, 2009; Tipping and Murray, 1999). Additionally, increased CO_2 levels may induce defense responses, for instance: increased production of oxydative compounds, which may explain why some species have been shown to have higher tolerance to herbicide under elevated CO_2 (Noctor and Mhamdi, 2017). In our study, the species with increased tolerance, *A. cordifolia,* displayed evidence of increased leaf waxiness when compared to the other study species (pers. obs. Tanja Lenz).

In other studies, responses to elevated CO_2 and herbicide application have similarly been shown to be species-specific (Manea et al., 2011; Ziska et al., 1999), herbicide-specific (Archambault et al., 2001), biomass or plant-age specific (Manea et al., 2011; Ziska et al., 2004, 1999; Ziska and Teasdale, 2000), as well as temperature and competition-level specific (Archambault et al., 2001). In addition, there have been differences observed between biotypes (Zhang et al., 2015). While this variability does not support a general trend towards increased herbicide tolerance under elevated CO_2 conditions, as initially predicted from early results (Manea et al., 2011; Ziska et al., 2004, 1999; Ziska and Teasdale, 2000), the variability does however highlight the urgent need to examine additional weed species across functional groups to determine the broader mechanisms of resistance including biochemical, morphological and genetic mechanisms (Fernando et al., 2016). The reported variability in tolerance to herbicide under future climate amplifies a number of concerns for land managers. Increased concentration of CO_2 in the atmosphere may not only change weed species' tolerance to herbicide but also facilitate novel disturbance regimes that promote spread of invasive plant species. For instance, predicted increase in fire frequency due to longer drought periods and higher temperatures may further support weed invasion (Espeland and Kettenring, 2018; Setterfield et al., 2018). Similarly, increased frequency of extreme events such as floods, storms and fires as predicted under climate change may open invasion windows for alien plant species (Leishman and Gallagher, 2015; Ramesh et al., 2017).

The smaller than expected effect of elevated CO_2 on herbicide efficacy in our study may be also due to the relatively low elevated CO_2 concentration (550 ppm) used compared to similar studies that typically used an elevated CO_2 concentration of 700 ppm. Similarly, Jabran and Doğan (2018) also reported no change in herbicide efficacy under a lower elevated CO_2 treatment (450 ppm). We chose to use 550 ppm as our elevated CO_2 treatment as it represents a more relevant timeframe for managers than 700 ppm (2100 under RCP 4.5 scenario, Stocker et al., 2013). Furthermore, the atmospheric CO_2 concentration of 700 ppm will result in drastic changes to global climate compared to the current climate (Meehl et al., 2007) which also makes using 700 ppm less relevant. However, Fernando et al. (2016) suggest that a tipping point for herbicide tolerance may exist, therefore it is important that future studies examine a CO_2 gradient rather than static levels.

5. Conclusion

Future elevated CO_2 levels may change the effectiveness of some herbicides in controlling weed species, but the level of herbicide tolerance is species-specific. Although so far no generalization can be made on herbicide efficacy under future CO_2 level, patterns are beginning to emerge as more species are examined. In our experimental study, vines and fast growing species appear most likely to show a decrease in glyphosate effectiveness when grown under elevated levels of CO_2. Of interest is the range of effectiveness of the double recommended rate of glyphosate on the fast-growing grasses (both C_3 and C_4). The grass species examined in this study, such as *E. erecta*, *C. clandestinum*, and B. *catharticus*, had very high mortality at double the recommended application rate. On the other hand shrubs such as *G. glaucophyllus* and *L. camara* displayed no difference in responses between CO_2 treatments at both recommended and double herbicide. We are not sure of the reasons for the variability of response to glyphosate for the species examined, thus we suggest that further work is needed to identify appropriate herbicide types and application rates under future CO_2 concentrations as well as the underlying mechanisms of modified herbicide efficacy under elevated CO_2. Due to the limited knowledge on how weeds respond to herbicide under increased CO_2 concentration, an appropriate level of monitoring and adaptive management is critical to reducing the risks.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jenvman.2018.08.050.

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